

EXPERIMENTS ON WINTER TERRITORIALITY OF THE AMERICAN KESTREL, *FALCO SPARVERIUS*

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DESPITE some salutary criticism (Lehrman, 1953) levied at the excessive use of hypothetical systems by the "ethologists," it seems that the methodology of these investigators offers possibilities for sound research into fields of animal behavior that have as yet been little explored by American scientists. For instance, Howell and Bartholomew (1952; 1954) have recently employed some of the ethologists' techniques in a meaningful way without resorting to the construction of elaborate hypotheses or becoming embroiled in a tortuous vocabulary. I refer, of course, to methods of *experimenting* with wild animals in the natural environment and, especially, to the introduction and manipulation of stuffed dummies, of various sorts of models, and captive, live animals into social situations involving wild creatures (see Tinbergen, 1948).

In the fall of 1952 I became interested in exploring the possibilities of using captives and stuffed dummies as aids to a comparative behavioral study of the long-winged hawks, genus *Falco*, on which I have been working for the past several years. Previously I had carried out a few cursory experiments with Peregrines (*Falco peregrinus*) and Gyrfalcons (*Falco rusticolus*) in Alaska with results indicating the desirability of a more thorough investigation than I could conduct in the wilderness areas where these two species were studied. I chose the American Kestrel (*Falco sparverius*) as the species for study because it is the commonest and most approachable falcon of southern California. I knew from casual observations that individuals of this species take up winter territories, and this was the aspect of behavior that I wanted to study.

It will be noted that I use the common name 'American Kestrel' in preference to the name 'Sparrow Hawk' for this falcon. The latter name was first applied to *Falco sparverius* in ignorance. Because it has had a long history of prior use for a true hawk, *Accipiter nisus*, the adoption of this name for our American falcon has been a constant source of confusion in the literature, especially when Latin names do not accompany the vernacular ones. The name 'American Kestrel' relates our species to its closest congener, *Falco tinnunculus*, and is more desirable from the standpoint of esthetics and conservation. Peterson (1947) makes a notable appeal for changing the common names of our North American falcons.

STUDY AREAS

Most of the experiments, and most of the observations on which the next section of the paper is based, were carried out in residential areas of Glendale, Hollywood, and West Los Angeles, California. Kestrels occurring in these districts were using vacant city lots for their winter hunting territories, and the experiments were conducted on these areas. A few experiments also were carried out in rural districts in the vicinity of Castaic, Los Angeles County, California, and on the Mojave Desert between Gorman and Lancaster. No differences were apparent in the behavior of urban and rural kestrels under comparable experimental conditions, but the rural kestrels were wilder and more difficult to work with.

ANNUAL CYCLE OF BEHAVIOR

Before discussing the actual experiments, it will be well to have in mind a brief sketch of the annual cycle of social organization in a kestrel population. There are no definitive studies on this subject, and the statements that I offer are based on my own casual observations over a number of years prior to 1952, and on intensive, year-around studies of 20 kestrels beginning in January, 1953, and continuing to the present.

Courtship.—In southern California mating behavior of most kestrels begins in January, although a few birds may be seen courting and engaging in copulatory behavior in late December. A few kestrels do not begin courtship until late February. Paired birds engage in a long pre-nesting association which is characterized by aerial displays (chiefly by the males), by social hunting by the pair, by courtship-feeding of the female, by mutual preening and billing, by characteristic chittering vocalizations, and by frequent acts of copulation throughout practically the entire period. Copulations become more and more frequent as egg-laying approaches (as many as six in half an hour have been counted) and end within a day after the last egg has been laid. This phase of the breeding cycle usually lasts twelve to fourteen weeks but can be prolonged considerably by a late spring, as was the case in 1954.

Although the pair bond in kestrels is strong, promiscuity is frequent on the part of both sexes. During the courting period adult kestrels appear to be more sociable toward each other than at any other time of the year, and the members of two or more pairs are not infrequently found together on the same area. (See Childs and Mossman (1952) for an account of such an occurrence.)

In one case closely observed by me, this sociability seemed to be directed only toward certain individuals. After a pair under observation had initial territorial conflicts with an intruding pair on their hunting and courting area, and after the female of the territory-holding pair had established complete

dominance over both intruders *by fighting*, the new birds were permitted to share the lot, and promiscuous matings were observed among these four birds. However, other stray kestrels that came to this lot were driven away by both the original and new pairs. The second pair finally took up a separate nesting territory near the end of the courting period, and the original pair was left in sole possession of the lot.

Occasionally during the courting period one finds an extra bird or two, usually a female, associating with an established pair. In January and February of 1954, a lot near the University of California campus was shared by two pairs and four unattached females. Territorial clashes were never seen.

Nesting.—In April or May a nesting site is occupied, usually near the hunting and courting area, but the only area defended during the nesting period is the immediate vicinity of the nest. Encroachments onto the former hunting area do not elicit attack. The eggs hatch in about 29 or 30 days (see Nice, 1954), and the young occupy the nest for about five weeks. The fledged young remain with their parents as a family unit in the vicinity of the nest for a variable time ranging from two weeks to a month or more. During most of this time the young continue to be fed by the parents to some extent. During the late summer the young finally are driven off by their parents, if they have not already strayed away on their own.

Social hunting groups.—Under favorable conditions, the siblings then form a social hunting group and occupy a given area for the rest of the summer. Several broods may band together, and I have seen as many as twenty juvenal kestrels hunting over a single field of 200 to 300 acres. I know of no instance where such an area has been defended by any of the juveniles.

Apparently the juveniles of all North American species of falcons form these hunting groups during the immediate post-nesting period. I have observed such groups of juvenal Peregrines and Gyrfalcons in Arctic Alaska, and twice in interior Alaska I encountered mixed hunting groups of juvenal Sharp-shinned Hawks (*Accipiter striatus*) and Merlins (*Falco columbarius*). Morlan W. Nelson, who is an accomplished falconer and a keen observer of wild falcons, first brought this phenomenon to my attention. He has observed it for a number of years among juvenal Prairie Falcons (*Falco mexicanus*) in Idaho. Mr. Nelson calls the area occupied by such a group the "hunting rendezvous". This social group is maintained until broken up by migration or, in the case of the kestrel at least, by aggressive territory-seeking adults coming into the area in the fall.

The only information concerning the onset of territorial behavior in first-year kestrels is provided by one male that was color-marked as a juvenile and observed continually from July to the following May. Territoriality was first

demonstrated experimentally on January 28 by the release of a trapped kestrel in his area. Previously, such releases had not elicited attack.

The winter period.—In southern California most resident kestrels maintain a permanent pair bond, occupying the same area throughout the year. Some local pairs break up in the fall, and the mates occupy separately-defended areas during the winter. Often their territories are adjacent and near their former nesting sites. A few breeding pairs in southern California leave the vicinity of their nests in the fall and are not seen again until late December or January. How far they move is not known.

The resident population is augmented in the fall and winter by migratory birds from the north and from the higher summer ranges in the mountains. The resident kestrels of urban districts usually constitute no more than one-fourth to one-half the maximal winter population, although the number of immigrants varies a great deal from year to year.

For the purposes of this study, winter territorial behavior is defined as the active defense of a hunting area by a pair or by an individual following the disintegration of the family groups. Most resident pairs begin to show such behavior in the last weeks of August. In migratory birds it begins with their impingements upon the territories of the resident kestrels. Active defense of a hunting area usually ends with the onset of the breeding cycle, and marked territoriality is not again seen until the nesting site is chosen.

PROCEDURE AND METHODS

In October, 1952, I began systematically recording the occurrence of kestrels in the study areas, locating territorial birds for later experimentation. By the end of the month it was apparent that many individuals consistently occupied the same lots. Birds that appeared to be the same individuals could be found on the same lots—usually on the same perches—at about the same time each day. Different perches, and sometimes different lots, were used at different times of the day. (After nearly three years of observation on individual birds, I can say that the constancy of individual patterns of daily activity is one of the most noticeable aspects of kestrel behavior. Miller's (1954) description of the roosting schedule of a female in this area is an excellent case in point.)

Trapping.—In order to make sure that I was observing the same individuals, I trapped some of the kestrels and color-marked them. Three types of traps were used with about equal success. One was a simplified version of the automatic bow-net recently described by Tordoff (1954). The other two were copies of ancient Persian traps used by falconers. The *balchatri* consists of a wire holding cage for live bait, over the top surface of which are attached slip nooses of lightweight nylon fishing leader. When a kestrel flies

down and strikes the cage, his feet become entangled in the nooses. The *dhogaza* is a lightweight net held vertically between two poles. The edge of the net is laced with a continuous line, the ends of which are attached to the upper ends of the poles. A hawk flying into this net in quest of the staked-out bait pulls the corners of the net loose from their fastenings, and it sacks around the bird. (See Meredith, 1943:442-447, for a complete description and diagrams of this trap.)

Marking.—Since October, 1952, I have trapped and banded forty kestrels. Some of these were color-marked with an acetone-base lacquer (airplane dope) on the dorsal surface of their central rectrices; others were marked by attaching colored jesses (leather leg straps) around their tarsi. The latter method is more satisfactory because the jesses remain intact for a longer time than the painted feathers, which are molted after one year.

A number of these marked birds were experimented with before they were trapped. Subsequent to their being trapped, most of them showed marked alterations in their responses to the same stimulus. Untrapped kestrels did not show such alterations even after many repetitions of the same stimulus. It was soon concluded that trapped birds did not give reliable results in most cases; therefore, all comparable experiments had to be carried out on untrapped birds.

Materials.—A male and a female were trapped and held in captivity for use in the experiments. These birds are referred to hereafter as the "lure-male," the "lure-female," or, collectively, as the "lure-birds." Another male and a female were secured for stuffed mounts. The male was prepared in the normal sitting posture; the female in the copulatory position with up-tilted tail. These birds are referred to hereafter as the "dummy-male," the "dummy-female," or as the "dummies."

The experiments reported below were carried out during the months of November and December, 1952, January, February, March, September, November, and December, 1953, and August, October, November, and December, 1954. The objective was to determine what kinds of response could be elicited from territorial kestrels during the winter by various presentations of the experimental objects on their hunting areas.

EXPERIMENTS WITH LIVE DECOYS

In the experiments involving the lure-birds, the procedure first used in 1952 was as follows: one of the lure-birds was tethered to a pyramidal, cloth-screened perch two feet in height from base to apex (Fig. 1). The lure-bird was tied on a short leash so that it could not touch the ground. If it attempted to fly away, it simply fell against the cloth screen on the side of the perch, a

position from which it could easily right itself. When a wild kestrel was sighted, the lure-bird was placed on the perch at a certain estimated distance from the territorial bird. Then the observer retreated, usually to a car or behind some concealing object, such a billboard, to observe. Subsequently this procedure was abandoned for the simpler one of staking the lure-bird on the ground at the end of a four-foot leash.

A great variety of responses was produced by the lure-birds, ranging from apparent indifference to violent and persistent attacks characterized by bodily



FIG. 1. Lure-male on the pyramidal perch near Gorman, California, December, 1952.

contact between the wild bird and the lure-bird. Some descriptions of experiments from my field notes will serve to illustrate the kinds of aggressive action elicited.

On November 13, 1952, at 8:20 a.m., a female that I had been observing for several weeks was sighted on her hunting area. She was perched on a telephone wire at the back of a lot about 50×50 yards in extent. The lure-male was set on his perch approximately 20 yards from the female. As I was

walking away from the lure-male in plain view of the female and before I was more than 10 yards distant, the female suddenly launched forth into a diagonal dive straight at the lure-male, passing just a few inches above his head. She made a sharp turn and alighted on the ground about two feet from the base of the lure-male's perch. Then she jumped up and hovered just over the lure-male's head for several seconds, finally flying back to the telephone wire, where she perched and screamed for a short time. Still screaming, she flew to a guy-wire on a telephone pole where she perched about fifteen feet directly above the lure-male. From this point she attacked again, striking the lure-male with her talons and knocking him off his perch. The female flew back to the guy-wire and then repeated her attack, knocking the lure-male off his perch a second time. At the end of this attack, she landed on the ground and sat looking at the lure-male, screaming for several seconds. After this action she flew back to the guy-wire. Again she dived and knocked the lure-male off his perch. By this time the action had been going on for five minutes, and I intervened to prevent injury to the lure-male. There were, however, no cuts or other signs of injury on his body. (I might add at this point that throughout these experiments the lure-birds frequently received blows as severe as the ones described here, but they were never injured in any way, and both were released in perfect condition at the end of the experiments.)

On the same day, at 8:55 a.m., I placed the lure-male in the territory of a male that I had been observing for several weeks. This territory consisted of a vacant lot about 300 $\times$ 400 yards in extent with three oak trees growing in it. The male used one of the oaks frequently for a perch and feeding station. At the beginning of this experiment, he was perched on top of a telephone pole on the north side of the lot. The lure-male was set out 100 yards away. There was no action for one or two minutes, the wild male appearing not to have seen the lure-male, which sat still. Presently the wild male flew from his perch and attacked a flock of four Killdeers (*Charadrius vociferus*) that were on the ground about thirty yards from him. He chased these birds out of the lot and disappeared from sight. At 9:00 a.m., I saw this same kestrel flying toward the lot from an unnoticed perch on the side of a hill to the east. He headed straight for the lure-male and hit him solidly with his talons on the first pass. He landed on the ground about three feet from the lure-male and screamed continually for several seconds. Then he began walking around the lure-male in a circle, drooping his inside wing so that the tips of the primaries dragged on the ground. This appeared to be some sort of threat-display. (Other males and females under similar circumstances have shown this same behavior.) After several seconds the male flew into the air again and, making a wide circle, he came in high over the lure-male, 'stooped', and knocked the lure-male off the perch. While the lure-male was dangling

over the side of the perch, the wild male alighted on the apex and sat there screaming. Each time the lure-male tried to right himself, the wild male knocked him back down with a blow from one foot while maintaining his stance on the perch with the other. Occasionally the wild male jumped up and hovered two or three feet above the perch, at which times the lure-male would right himself only to be knocked down promptly by the wild male. After ten minutes had elapsed, I intervened, and the wild male flew to his perch in the oak tree.

On December 8, 1952, I set the lure-male in the area of a wintering pair, at 9:05 a.m. Both wild birds immediately started circling in the air over the lure-male, screaming. In less than one minute the wild male started stooping at the lure-male and striking him with closed fists. The female continued to fly about in an excited manner higher up. She did not stoop at the lure-male. Forty minutes later, when I moved in to retrieve the lure-male, these birds had not lessened the intensity of their actions, except for brief pauses.

On October 17, 1954, at 8:42 a.m., I set the lure-female on the ground in the territory of a resident female. The wild female was 35 yards away. She watched the lure-female intently for a few seconds and bobbed her head up and down. At 8:45 a.m. the wild female flew toward the lure-female, dropped to the ground, and caught an insect about 10 yards away from her. She flew back to her perch on a fence and ate the insect. There was no further action for ten minutes, after which the lure-female was removed.

The same day, at 9:56 a.m., I set the lure female in the area of a wintering female. The wild female was 50 yards away. Immediately she flew down and struck the lure-female a blow with her closed feet. She circled around once more and landed on the ground two feet away from the lure-female. Then she charged in and grabbed the lure-female by her legs, pinning her to the ground on her back. The wild female held the lure-female in this position for several seconds and then flew into the air screaming. She repeated variations of this attack for ten minutes, when I intervened.

DISCUSSION

These five accounts give an idea of the variability of the responses elicited by the lure-birds. Actually no two birds reacted with an identical pattern of behavior, but for the purpose of presenting the data quantitatively, it is convenient to group the results into three categories. Some birds remained on their perches, continued hunting activities, or in other ways showed no change in their behavior when the lure-birds were presented on their areas. Others screamed and dived at the lure-birds, always staying above them and never coming into bodily contact. The most aggressive birds not only screamed and

dived at the lure-birds but also actually struck them with their feet in the air or landed on the ground and grappled their legs, pinning them down.

Tables 1 and 2 summarize the data in these three categories of behavior. Inspection of these tables reveals no differences among the four experimental

TABLE 1
RESPONSES OF FREE-LIVING KESTRELS TO THE LURE-MALE

Experimental Groups	Types of Attack			Totals
	Striking and Grappling with feet	"Stooping" without bodily contact	None	
Single Males	8	3	3	14
Paired Males	10	1	3	14
Paired Females	8	4	2	14
Single Females	11	4	4	19

groups in their responses to the lure-male, but there is a marked difference between the males and the females in their responses to the lure-female. Only one-third of the single males actually came into bodily contact with the lure-female in comparison to about three-fifths of the females which did. None of

TABLE 2
RESPONSES OF FREE-LIVING KESTRELS TO THE LURE-FEMALE

Experimental Groups	Types of Attack			Totals
	Striking and Grappling with feet	"Stooping" without bodily contact	None	
Single Males	4	4	4	12
Paired Males	0	5	5	10
Paired Females	8	2	0	10
Single Females	9	4	3	16

the paired males hit the lure-female, but four-fifths of the paired females did. The difference between the frequencies of all highly aggressive males and all highly aggressive females of table 2 gives a chi square value greater than that required for P to equal the one per cent level of significance.

EXPERIMENTS INVOLVING MOUNTED MODELS

Usually the dummies were set out in the territories on a six-foot rod that was stuck into the ground, but in a few instances they were placed on the ground or on fence posts, and in one case in the top of a pepper tree (*Schinus molle*).

The experiments with the dummies produced a much smaller number of responses. The dummy-male was presented to seven single males, four single females, and one resident pair. None of these birds showed any reaction to the dummy-male. The dummy-female was presented to eight single males, three single females, and two resident pairs. The dummy-female elicited responses three times. One of the females that had been strongly aggressive toward the lure-male during a previous experiment stooped over the dummy-female when it was placed on the ground. On a subsequent day when the dummy-female was set up on the six-foot pole, the same female dived at the dummy and hit it several times in five minutes.

On February 7, 1953, about 4:30 p.m., a male and a female were observed in courting display on a lot that had been the female's hunting area for the past three and one-half months. The female flew out of the area at my approach, but the male remained. I placed the dummy-female in the uppermost branches of a pepper tree growing in the lot. In the meantime the male was flying high overhead. As soon as I retired to watch, the male flew down and hovered just above the dummy-female for several seconds and then flew away.

EXPERIMENTS WITH MODELS AND LURE BIRDS

The experiments involving combined presentations of the lure-male and the dummies revealed some interesting aspects of behavior. In these experiments three different males that had previously shown strong aggressive actions toward the lure-male were used. In the first experiment, in which the lure-male was first presented singly and the dummy-male then substituted for it immediately afterward, the wild male again initiated violent attacks on the lure-male. When the dummy was substituted, the wild male continued attacking it just as vigorously as before and continued to do so for nearly ten minutes, until scared away by a pedestrian.

In the second experiment, the wild male also attacked the lure-male when it was set out alone, but when the dummy-female was presented simultaneously above the lure-male on the six-foot rod, the attacks were switched to her, and these continued in excess of ten minutes. During this time the wild male did not attack the lure-male once, but the dummy-female was hit so hard that its head fell off.

The other experiment of this series occurred by chance. The dummy-male

had been set out 100 yards from a resident male, and there had been no action for about five minutes. Then the lure-male suddenly began screaming the common *killy-killy* cry from his perch inside my car. The resident male immediately answered with a corresponding call and flew directly at the dummy-male, striking it roughly with his talons on the first stoop. Prior to this action there had been no indication that the wild male was aware of the presence of the dummy-male. The lure-male continued to scream at intervals for about five minutes, and during this time the dummy-male was struck many times by the wild male, which displayed even greater aggressiveness than he had shown toward the lure-male in previous experiments.

DISCUSSION

Comparing the results obtained with the lure-birds to those obtained with the dummies, one can say that movement or "aliveness" is a stronger releaser of territorial aggressiveness in kestrels than are form or plumage pattern. This conclusion is also supported by field observations. If a stray kestrel flies quietly into the territory of another bird, and then sits still in a low, inconspicuous place and does not attempt to hunt, the resident bird frequently will not attempt to drive it away; but if the intruder flies about over another bird's territory or attempts to hunt there, it is nearly always attacked.

The last experiment described in the foregoing section shows strikingly the effect of vocalizations on the aggressive behavior of territorial kestrels. Field observations indicate that the *killy-killy* cry is used by resident kestrels to advertise their presence, and frequently this vocalization alone is enough to cause an intruder to leave the area. If an intruder vocalizes, the resident will attack at once.

The differences in the reactions of males and the reactions of females to the lure-female reflects a fundamental aspect of the social behavior of this species. In any social situation involving a pair of kestrels, the male is nearly always subordinate to the female. The female has first right to food taken by herself or by the male. If the male does not present his food to the female, she may take it from him, in which case he does not offer resistance. However, the female does not often enforce her dominance for the food except in the breeding season. The female has first right to favorite perches and roosts. The female accepts or rejects the male in the initial pair-formation, and she releases and controls copulatory behavior. The male inspects a number of nesting sites, but it is the female that chooses the one in which the eggs are laid.

Sherman (1913) is apparently the only one who has recorded detailed observations on the nest-life of the American Kestrel. She presents some

evidence to show that this fundamental difference between the sexes first appears when the birds are nestlings. After the young which she was observing were old enough to feed themselves, the females always ate first and took the most, gaining weight faster than the males. If a hand or a stick was thrust into the nest the males reared back on their tails and opened their beaks, but the females struck out with their feet. I have applied this same test to fledgling Peregrines, Gyrfalcons, and Prairie Falcons and, while the results are not invariable, in general, the same relationship holds for these species. Sherman (1913:410) says, "This yielding of their lawful share of food by the males may have its origin in their disposition in mature life to give the food they bring to their mates." I am inclined to think the statement should be reversed—that the bringing of food to the female and the courtship-feeding of mature life are developments from the social tendencies of nestling life.

It becomes important to learn how much the behavior of males toward their mates is modified by the social milieu of nestling life. For instance, would a brood of all males produce individuals showing the same submissiveness to females that a mixed brood would produce?

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SUMMARY

Winter territoriality is a prominent feature in the behavioral cycle of the American Kestrel (*Falco sparverius*). It functions primarily to maintain an adequate hunting ground for the individual. Experiments employing a captive, adult male, a captive female, a stuffed dummy-female, and a stuffed dummy-male were carried out to study this behavior. The reactions of wild kestrels toward the experimental objects placed in their territories ranged from apparent indifference to the most violent and persistent kinds of attack. There was no measurable difference between the reactions of males and females to the captive male, a majority of both sexes being highly aggressive; females also attacked the captive female as frequently as they did the captive male, but males showed a marked decrease in the frequency of their attacks on the captive female, especially of attacks resulting in bodily contact. This difference between the sexes is the reflection of a masculine submissiveness which has its earliest manifestations during nestling life. A comparison of the results produced by the live captives and the dummies indicates that movements and vocalizations are stronger releasers of aggressive behavior than are form or pattern *per se*.

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